

SQUIRRELS AS PREDATORS

J. R. Callahan¹

ABSTRACT—A literature review and field observations indicate that most sciurids are facultative predators on small vertebrates. This behavior is documented for at least 30 sciurid species in 5 genera. The frequency of predation apparently is influenced by various factors including climate, season, gender, reproductive condition, and availability of plant sources for certain nutrients such as calcium and nitrogen. Although sciurids assimilate as much energy from animal foods as do obligate carnivores, behavior associated with predation appears to be less efficient in sciurids and may rely partly on prey habituation and other adaptive behaviors.

Key words: squirrel, Sciuridae, predator, carnivore, omnivore.

Predators utilize various strategies that maximize the probability of successful prey capture while minimizing the probability of injury. Sciurid rodents, many of them facultative and opportunistic predators, are not morphologically specialized for this role and should therefore possess a wide variety of adaptive attack behaviors. As discussed below, one of these behaviors observed in tree squirrels appears similar to insinuation (Curio 1976), a strategy more often associated with invertebrates than with mammals.

Predation, as defined here, means the killing and eating of active vertebrates (including conspecifics) or other relatively large, mobile prey by free-living squirrels. This definition excludes the consumption of eggs, nestling birds, small insects, or any animal that is already dead. Prey offer some resistance; eating carrion or aphids is similar to browsing. Predation also excludes killing that appears unrelated to feeding, as in defense of the nest (Harris 1985) or as a reproductive strategy (Balfour 1983, Weissenbacher 1987). Finally, behavior of caged squirrels is often abnormal and is excluded here as evidence of predation, although it can provide clues to dietary deficiencies.

Not all biologists accept the idea of squirrels as frequent predators. Despite the 70-year literature record summarized in Table 1, O'Donoghue's recent (1991) finding that squirrels are the chief predator of juvenile snowshoe hares elicited general "shock" (C. Krebs, per-

sonal communication). There is universal acceptance that squirrels eat meat; the question is how they obtain it. Squirrels are often seen eating carrion on roads but are rarely seen attacking live prey. Stomach contents analysis may overlook vertebrate flesh and cannot distinguish live prey from carrion. Thus, each new observation of a squirrel acting like a predator becomes a journal note (see Literature Cited). Although most of these notes imply that such behavior is aberrant, collectively they describe a significant component of the sciurid repertoire. The same feeding adaptations that enable squirrels to crack nuts are sufficient for opening skulls (Landry 1970).

TREE SQUIRRELS.—The following field observation (which prompted this review) adds a species to the list of reported sciurid predators. On 6 April 1979, I saw a lactating female western gray squirrel (*Sciurus griseus*) stalk and attack an adult mountain quail (*Oreortyx pictus*) in mixed-conifer forest at Black Mountain, Riverside County, California, elevation 1800 m. The quail was standing on a 60-cm stump at the edge of a clearing; five or six other quail were nearby. None of the quail appeared to react as the squirrel crossed the clearing in an odd, crouched posture, rustling the pine needles and leaves loudly enough to attract my attention. When it was 20 cm from the stump, it leapt up and pounced on the quail. After a brief struggle, the quail escaped and the coxey moved off. In six years in the same area, on two other occasions

¹Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico 87131. Mailing address: Box 3140, Hemet, California 92346

TABLE 1. *Behavioral aspects of predation by squirrels.* This table is limited to behavior of free-living squirrels and includes only predation and predation attempts as defined in text.

Species	Prey	Source
TREE SQUIRRELS		
Eastern gray squirrel (<i>Sciurus h. mollivossis</i>)	Conspecifics, birds	Holm (1976), Bailey (1923)
Western gray squirrel (<i>Sciurus griseus</i>)	Mountain quail; unidentified small mammal (<i>Peromyscus</i> ?)	This paper
Eastern fox squirrel (<i>Sciurus niger</i>)	Dove, blue jay, other birds	Borell (1961), Seton (1929), Shaffer and Baker (1991)
European red squirrel (<i>Sciurus vulgaris</i>)	Squirrels, birds	Gurnell (1987), Schlogel (1985)
Douglas squirrel (<i>Tamiasciurus douglasi</i>)	Ground squirrels	Roest (1951)
Pine-Red squirrel (<i>Tamiasciurus hudsonicus</i>)	Chipmunks, tree squirrels, cottontail, snowshoe hare, mourning dove, other birds	Hatt (1929), Seton (1929), Hamilton (1934), O'Donoghue (1991), Nero (1987), Taylor (1988)
Little green squirrel (<i>Actosciurus poeisis</i>)	Frog (live?)	Emmons (1980)
GROUND SQUIRRELS		
Whitetail antelope squirrel (<i>Ammospermophilus leucurus</i>)	Pocket mouse, kangaroo rat, lizards	Bradley (1968), Morgart (1985)
Nelson antelope squirrel (<i>Ammospermophilus nelsoni</i>)	Lizards	Hawbecker (1947)
Yellow-bellied marmot (<i>Marmota flaviventris</i>)	Conspecifics	Armitage et al. (1979)
Caldworn ground squirrel (<i>Spermophilus beecheyi</i>)	Ground squirrels, rabbits, pocket gophers, moles, birds, lizards	Grinnell & Storer (1924), Fitch (1948), Sumner & Dixon (1953), Sandberg and Banta (1973), Trulio et al. (1986)
Belding ground squirrel (<i>Spermophilus beldingi</i>)	Chipmunks, other small mammals, juncos, warbler	Sharsmith (1936), Howell (1938), Sherman & Morton (1979), Michener (1982)
Snailik (<i>Spermophilus citellus</i>)	Field mice, birds, snakes, conspecifics	Calinescu (1934), Herzog-Straschil (1976)
Columbian ground squirrel (<i>Spermophilus columbianus</i>)	Fish (live?)	Howell (1938)
Franklin ground squirrel (<i>Spermophilus franklini</i>)	Voles, domestic fowl, ducks, other birds	Polder (1955), Johnson (1922), Howell (1938), Sows (1948), Choromanski & Sargeant (1982)
Cockle-eyed ground squirrel (<i>Spermophilus lateralis</i>)	Voles, deer mice, chipmunks, juncos, lizards	Cameron (1967), Tevis (1953)
Merriam ground squirrel? (<i>Spermophilus merriami</i>)	Cottontail	Packard (1958)
Reardon (Yellow) ground squirrel (<i>Spermophilus reardonianus</i>)	Sparrows	Bradley (1968)
Towhee ground squirrel (<i>Spermophilus towheensis</i>)	Conspecifics	Michener (1982)
Flined ground squirrel (<i>Spermophilus tridecemlineatus</i>)	Rabbits, birds	Bridgewater & Penny (1966), Bailey (1923)
Arctic ground squirrel (<i>Spermophilus undulatus</i>)	Conspecifics, snowshoe hare, Siberian lemming	O'Donoghue (1991), Holmes (1977), Boonstra et al. (1990), Michener (1982)
Cook squirrel (<i>Spermophilus arizonae</i>)	Bobcats, ravs	Cook & Henry (1940)

TABLE 1. Continued.

Species	Prey	Source
Washington ground squirrel (<i>Spermophilus washingtoni</i>)	Conspecifics	Mcorn (1940)
South African ground squirrel (<i>Xerus inauris</i>)	Domestic fowl, other birds, turtles, other reptiles	Shortridge (1934), Ryan (1957)
African ground squirrel (<i>Xerus rutilus</i>)	Cobra	Stiles (1957)
CHIPMUNKS		
Cliff chipmunk (<i>Tamias dorsalis</i>)	Crabs	Jenkins 1959
Merriam's chipmunk (<i>Tamias merriami</i>)	Lizards, sparrows	Larson (1956)
Least chipmunk (<i>Tamias minimus</i>)	Tree swallows	Lederle et al. (1955)
Asian chipmunk (<i>Tamias sibiricus</i>)	Voles, birds, lizards, frogs	Ognev (1966)
Eastern chipmunk (<i>Tamias striatus</i>)	Conspecifics, voles, swallows, starling, snakes, frogs, salamander	Krull (1969), Seton (1929), Ginevan (1971), Hesterberg (1940), Harriot (1940), Shackleford (1966), Torres (1937)

I saw a western gray squirrel stalk a bird briefly but then retreat without completing a predation attempt. On 1 April 1993, S. B. Compton (personal communication) saw a western gray squirrel with a small, live mammal in its mouth, the size of a young *Peromyscus*, beside a road in the San Jacinto Mountains (2100 m).

Ingles (1947), Cross (1969), Jaeger (1929), and Stienecker and Browning (1970) reviewed the food habits of the western gray squirrel but reported no predation (although the latter found feather fragments in one stomach). At least six other tree squirrel species take live prey (Table 1), but the frequency of such behavior is unknown. Meat constitutes 2–11% of the diet of the eastern gray squirrel, *Sciurus carolinensis* (Packard 1956, Nixon et al. 1965); however, stomach contents analysis does not reveal how meat was obtained. Moreover, squirrels are erratic predators and not all studies are in agreement. Whereas Borell (1961) and O'Donoghue (1991) reported predation by the fox squirrel (*S. niger*) and red squirrel (*Tamiasciurus hudsonicus*), respectively, Reichard (1976) saw no predation by either species.

It is not entirely clear whether a tree squirrel attacks live prey to obtain meat per se or calcium and/or phosphorus from the bones. Shaffer and Baker (1991) noted that a fox squirrel, after

killing a young blue jay, avoided the skeletal muscle and gnawed on the joints and bones near the surface of the skin. This is in agreement with other reports of tree squirrels eating bone and antlers (Cross 1969, Leach 1977). In other cases, however, sciurids have consumed specific prey organs such as the brain (Hamilton 1934, Elliott 1978) or viscera (Hesterberg 1940), or the flesh of the head (Holm 1976).

Predation by tropical tree squirrels appears to be rare. Emmons (1980) saw no predation by any of nine African species, although one *Aethosciurus* stomach contained a frog (Table 1). Glanz et al. (1982) wrote that *Sciurus granatensis* rarely eats animal foods. *Paraxerus cepapi* eats eggs, nestlings, and insects, but apparently no prey as defined here (Shortridge 1934); male *P. cepapi* sometimes kill juvenile conspecifics, but Weissenbacher (1957) regards this as a reproductive strategy rather than predation per se. Viljoen (1975) reported no predation by *Funisciurus congicus*. Small arthropods and annelids are the only known animal foods of *Sundasciurus lowii*, *Lariscus obscurus*, *Callosciurus melanogaster* (Whitten 1951), *Callosciurus erythraeus* (Setoguchi 1990), and *Tamias meclellandi* (Moore and Tate 1965). Borges (1990) stated that *Ratufa* is an obligate herbivore.

The infrequency of scinrid predation in the tropics could be an artifact based on the geographic distribution of observers. Certain other mammals, however, are facultative predators in only part of their geographic range (e.g., the chimpanzee; Curio 1976). For scinrids, the most likely explanations include the following: (1) certain tropical plants and tree barks are rich in calcium and other nutrients (see Borges 1990); (2) carnivory in the tropics may be associated with increased numbers of stomach nematodes (Emmons 1980); (3) colder climate necessitates a high-fat diet; or (4) facultative predation is partly a learned behavior that can spread through a local population, but need not occur over the entire range of a species. The first hypothesis is supported by the fact that tropical tree squirrels turn to predation when caged and deprived of a normal diet (e.g., Keshava Bhat 1980).

GROUND SQUIRRELS.—Meat (live prey and carrion) is a major food source for ground squirrels worldwide, although fewer data are available regarding Old World species. Table 1 lists reports of predation by 18 species of *Spermophilus*, *Ammospermophilus*, *Marmota*, and *Xerus*. A possible exception is the Mohave ground squirrel (*Spermophilus mohavensis*), which has been studied intensively (Leitner et al. 1991) but is not known to take live vertebrate prey. The cheek pouches and stomachs of four *Sciurotamias davidianus* specimens contained only plant material (Callahan and Davis 1982), but no field data on this endemic Chinese genus are available.

FLYING SQUIRRELS.—The southern flying squirrel (*Glaucomys volans*) eats eggs, nestlings, and carrion (Bailey 1923, Landry 1970), but not consistently (Harlow and Doyle 1990). I have found no record of predation as defined here.

CHIPMUNKS.—The eastern chipmunk (*Tamias striatus*) and the Asian chipmunk (*T. sibiricus*) take a variety of prey (Table 1). Lederle et al. (1985) reported that least chipmunks (*Tamias minimus*) prey upon adult tree swallows, as well as eggs and young. Jenkins (1989) observed cliff chipmunks (*Tamias dorsalis*) in coastal Sonora, Mexico, eating crabs and other marine invertebrates in tide pools; because the exact size of the crabs was not documented, this is a borderline case of "predation." Larson (1986) reported that the Murray chipmunk (*Tamias merriami*) occasionally eats lizards and birds. The lodgepole

chipmunk (*Tamias speciosus*) is somewhat specialized as an arboreal nest predator (Grinnell 1905, Grinnell and Storer 1924), but it has been reported to eat eggs rather than adult birds. Similar behavior is reported for the Uinta chipmunk (*Tamias umbrinus*) (Smith and Anderson 1982).

SIGNIFICANCE.—There are really two questions here: (1) Why eat meat? (2) Why catch it while it is still alive?

A frequent answer to the first question is that squirrels, especially reproductive females, may need a concentrated source of protein and/or certain minerals. This view is supported by studies of calcium self-selection by male and female Malabar giant squirrels (*Ratufa indica*) (Borges 1990). Smith (1968) and Carlson (1940) reported that only pregnant and lactating tree squirrels regularly eat animal food. Studies cited by Gurnell (1987) showed that female tree squirrels cannot always obtain enough calcium, phosphorus, sodium, or nitrogen from a diet of seeds. Goodrum (1940) speculated that female squirrels may need meat to reproduce successfully. Keymer and Hime (1977) reported a wild European red squirrel (*Sciurus vulgaris*) with nutritional osteodystrophy, suggesting that dietary calcium may be a limiting factor in the distribution of certain species.

A second viewpoint is that the seasonal increase in meat consumption, whether of live prey or carrion, compensates for a seasonal decline in the quality of plant food (especially protein content) and is not specifically related to reproduction. Nutrient density and water content of plants eaten by squirrels decline in spring and summer (Bintz 1984). In the Mojave Desert, plant foods evidently contain sufficient calcium, but nitrogen is likely to be limiting for desert ground squirrels that are active year-round (Karasov 1985); conversely, tree squirrels in more mesic environments have fungi available as a source of nitrogen but are more likely to need calcium seasonally (Carlson 1940, Coventry 1940, Keymer and Hime 1977). Phosphorus also may be a factor in food selection; Cano and Colomé (1986) attribute the consumption of carrion by cattle in parts of South Africa to phosphorus-deficient soils. When kept on a herbivorous diet, Belding's ground squirrels select plant parts highest in protein and water (Eshelman and Jenkins 1989). Gurnell (1987) wrote that tree squirrels use animal food mainly in the summer. Weeks and Kirkpatrick

(1978) studied the "salt drive" phenomenon in fox squirrels and marmots. Clark (1968) found that the proportion of animal food in *Spermophilus richardsoni* stomachs increased from 3% in April to 24% in August. Tevis (1953) reported a similar phenomenon for chipmunks and golden-mantled squirrels.

A third hypothesis is that predation by squirrels is often incidental to killing for some other reason, usually territorial defense or reproductive competition. In other words, once the other animal is dead, it provides an energetic bonus that can be consumed without further risk. This explanation applies mainly to certain ground squirrel species (Holmes 1977, Michener 1982, Balfour 1983, Harris 1985).

The other question concerns the advantages of live prey. Carrion contains protein and other nutrients, and it does not run away or fight back. Carrion also has disadvantages: nutrient content diminishes due to desiccation and removal of organs (by the original predator or by earlier scavengers); carrion occurs in high-risk situations (near ravens, predator dens, or cars); and it may contain harmful bacteria. But the worst thing about carrion is that it may not be available when needed. Most reports of scavenging by free-living squirrels involve road kills, an artificially concentrated phenomenon.

"Quasi-prey," such as small frogs and most arthropods, are a fairly safe bet when available. Nestling birds are somewhat more difficult because of nest defense by the parents (Smith 1970, Shaffer and Baker 1991). The hardest prey to explain are adult birds, rodents, and rabbits, since these have defenses sufficient to inflict injury on a squirrel. The prevalent view is that squirrels turn to live prey only as an "emergency" food source (Reichard 1976) when other resources are depleted. This view implies that predation is a freakish event that has no real bearing on the squirrel's role in the food web. To paraphrase Landry (1970), isolated events of carnivory do not a carnivore make. (To support this statement, Landry cites an observation of a deer eating a rabbit.)

Again, however, a growing body of evidence suggests that predation is a normal component of the feeding repertoire for most sciurids, at least outside the tropics. This does not imply that squirrels are fundamental predators, but simply that they are opportunistic. One reviewer of this paper commented that squirrels are "lousy predators." Undoubtedly this is true

to some extent; but neither the apparent low success rate nor the situation-specific response to potential prey is unique to squirrels. Both phenomena are reported for many obligate predators as well (Curio 1976). Moreover, Karasov (1982) found that antelope ground squirrels assimilate energy from animal foods just as efficiently as do obligate predators.

There is a learned component in predator recognition and avoidance by birds and mammals (Curio 1976, Robinson 1980). It would be a waste of energy for rabbits to avoid deer, for instance, even though one deer ate one rabbit. But if squirrels undergo dietary stress every year and begin eating peculiar things, one might expect prey to catch on. The limited evidence available suggests this is not the case. Birds apparently respond to models of squirrels near their nests (Holson et al. 1988)—a not unexpected result, since nest predation is a frequent sciurid behavior. Smith (1970) reported that two cactus wrens (*Campylorhynchus brunneicapillus*) attacked and injured a Harris antelope squirrel (*Amnospermophilus harrisii*) near an old nest. In other contexts, however, birds and other potential prey often seem to ignore squirrels.

A clue to this blasé response may be found in the "stalking" behavior occasionally observed in tree squirrels, including the western gray squirrel as described above. This behavior is not associated with the routine operation of nest robbing but seems limited to the relatively infrequent attempts on larger prey. Klugh (1927) similarly wrote that red squirrels sometimes appear to stalk grouse or partridges, repeatedly advancing on the bird and then retreating. This is similar to my own observations of western gray squirrels reported above. The squirrel engaged in this near-caricature of a stalking predator is actually more conspicuous than usual (at least to the human observer). It is possible that the effect of obvious repeated stalking is to habituate potential prey.

Most published reports of sciurid predation are brief notes, since it is difficult to conduct a quantitative study of any rare phenomenon. However, some tentative inferences can be drawn. The proximate significance of stalking may be that the squirrel is showing conflict behavior, advancing and then retreating if the bird or other prey appears in a position to defend itself. In the ultimate sense, the squirrel should benefit from this behavior if its effect is to condition the local prey population to disregard

stalking squirrels. If most squirrels acting like predators do not follow through, then prey should learn not to respond. This behavior is analogous to the hoarding of nuts, in that the squirrel is hoarding prey confidence. Later, when normal food items are in short supply, the squirrel can exploit this conditioning. In the longer term, selection for such behavior potentially represents an entry point to a new feeding niche, particularly in marginal habitats where tree squirrels may be more likely to resort to predation.

ACKNOWLEDGMENTS

This paper was begun with the assistance of an NSF grant (BNS 75-17469) to the University of Georgia, and was resumed under a 1990-91 Theodore Roosevelt Memorial Grant to the author.

LITERATURE CITED

- ACCORN, J. R. 1940. Life history notes on the Pinta ground squirrel. *Journal of Mammalogy* 21: 160-170.
- AMMIFACE, K. B., D. JOHNS, AND D. C. ANDERSEN. 1979. Cannibalism among yellow-bellied marmots. *Journal of Mammalogy* 60: 205-207.
- BAILEY, B. 1923. Meat-eating propensities of some rodents of Minnesota. *Journal of Mammalogy* 4: 129.
- BALFOUR, D. 1983. Infanticide in the Columbian ground squirrel, *Spermophilus columbianus*. *Animal Behavior* 31: 949-950.
- BENZ, G. L. 1984. Water balance, water stress, and the evolution of seasonal torpor in ground-dwelling sciurids. Pages 142-165 in J. O. Murie and G. R. Michener, eds., *The biology of ground-dwelling squirrels*. University of Nebraska Press, Lincoln.
- BOONSTEEL, R. C., J. KREBS, AND M. KANTER. 1990. Arctic ground squirrel predation on collared lemmings. *Canadian Journal of Zoology* 68: 757-760.
- BOULEE, A. E. 1961. Fox squirrel attacks mourning dove. *Journal of Mammalogy* 42: 101.
- BOULEE, R. M. 1990. Sexual and site differences in calcium consumption by the Malabar giant squirrel, *Ratufa molle*. *Oecologia* 85: 50-56.
- BOULANGER, W. G. 1965. Food habits of the antelope ground squirrel in southern Nevada. *Journal of Mammalogy* 46: 14-24.
- BRIDGES, D. D. AND D. F. PENNY. 1966. Predation by *Citellus tridecemlineatus* on other vertebrates. *Journal of Mammalogy* 47: 345-346.
- CHODURA, K. J. 1994. Evolutionäre, biologische und bioökologische Einordnung über die Gattung *Citellus* (Dipos. = Thomomys). *Zeitschrift für Säugetierk.* 9: 57-113.
- CHODURA, K. J. AND R. DAVIS. 1982. Reproductive tract and conditions in females of the Chinese rock squirrel *Sciurus sinensis* *decaudatus*. *Journal of Mammalogy* 63: 12-27.
- CHODURA, K. J. AND M. 1987. *Long-term observation of the gold mouse lemur (Primate, Strepsirrhini)*. 18 pp.
- CASO, R. J., AND J. S. COLOMIE. 1956. Page 665 in *Microbiology*, West Publishing Co., St. Paul, Minnesota.
- CARLSON, A. J. 1940. Eating of bone by the pregnant and lactating gray squirrel. *Science* 91: 573.
- CHOROMANSKI, J., AND A. B. SARGENT. 1952. Gray gophers and prairie ducks. *North Dakota Outdoors* 45: 6-9.
- CLARK, T. W. 1968. Food uses of the Richardson ground squirrel (*Spermophilus richardsonii elegans*) in the Laramie Basin of Wyoming. *Southwestern Naturalist* 13: 245-249.
- COOK, A. H., AND W. H. HENRY. 1940. Texas ground squirrels catch and eat young wild turkeys. *Journal of Mammalogy* 21: 92.
- COVENTRY, A. F. 1940. The eating of bone by squirrels. *Science* 92: 128.
- CROSS, S. P. 1969. Behavioral aspects of western gray squirrel ecology. Unpublished doctoral dissertation, University of Arizona, Tucson. 165 pp.
- CURIO, E. 1976. The ethology of predation. Springer-Verlag, New York.
- ELLIOTT, L. 1978. Social behavior and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack Mountains. *Smithsonian Contributions to Zoology* No. 265. 107 pp.
- EMMONS, L. H. 1980. Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecological Monographs* 50: 31-54.
- ESHELMAN, B. D., AND S. H. JENKINS. 1989. Food selection by Belding's ground squirrels in relation to plant nutritional features. *Journal of Mammalogy* 70: 546-552.
- FITCH, H. S. 1948. Ecology of the California ground squirrel. *American Midland Naturalist* 39: 513-596.
- GINEVAN, M. 1971. Chipmunk predation on bank swallows. *Wilson Bulletin* 83: 102.
- GLANZ, W. E., R. W. THORINGTON, J. MADDEN, AND L. R. HEANEY. 1982. Seasonal food use and demographic trends in *Sciurus granatensis*. Pages 239-252 in E. Leigh, A. S. Rand, and D. M. Windsor, eds., *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C.
- GOODRUM, P. D. 1940. A population study of the gray squirrel in eastern Texas. *Texas Agricultural Experiment Station Bulletin* 591: 1-34.
- GRINNELL, J. 1908. The biota of the San Bernardino Mountains. University of California Publications in Zoology 5: 1-170.
- GRINNELL, J., AND T. L. STORER. 1924. *Animal life in the Yosemite*. University of California Press, Berkeley.
- GURNELL, J. 1987. *The natural history of squirrels*. Facts on File Publications, New York.
- HAMILTON, W. J. 1934. Red squirrel killing young cottontail and young gray squirrel. *Journal of Mammalogy* 15: 322.
- HARLOW, R. E., AND A. T. DOYLE. 1990. Food habits of southern flying squirrels (*Glaucomys colans*) collected from red-cockaded woodpecker (*Picoides borealis*) colonies in South Carolina. *American Midland Naturalist* 124: 187-191.
- HARRIOTT, S. C. 1940. Chipmunk eating a red-bellied snake. *Journal of Mammalogy* 21: 92.
- HARRIS, M. A. 1985. Possible occurrence of inter-specific killing by a Columbian ground-squirrel, *Spermophilus columbianus*. *Canadian Field-Naturalist* 99: 250-252.
- HUNT, R. T. 1929. The red squirrel: its life history and habits. *Roosevelt Wildlife*. *Annals* 2: 1-46.

- HAWBECKER, A. C. 1947. Food and moisture requirements of the Nelson antelope ground squirrel. *Journal of Mammalogy* 28: 115-125.
- HERZIG-STRASCHIL, B. 1976. Nahrung und Nahrungserwerb des Ziesel. *Acta Theriologica* 21(7): 131-139.
- HESTERBERG, G. A. 1940. Chipmunk eats frog. *Journal of Mammalogy* 31: 350-351.
- HOBSON, K. A., M. L. BOUGHART AND S. G. SEALY. 1985. Responses of naive yellow warblers to a novel nest predator. *Animal Behaviour* 36: 1823-1830.
- HOLM, R. F. 1976. Observations on a cannibalistic grey squirrel. *Natural History Miscellany* (Chicago Academy of Sciences) 197: 1-2.
- HOLMES, W. G. 1977. Cannibalism in the Arctic ground squirrel (*Spermophilus parryi*). *Journal of Mammalogy* 58: 437-438.
- HOWELL, A. H. 1938. Revision of the North American ground squirrels. *North American Fauna* 56: 1-256.
- INGLES, L. J. 1947. Ecology and life history of the California gray squirrel. *California Fish and Game* 33: 139-155.
- JAEGER, E. C. 1929. *Denizens of the mountains*. Charles C. Thomas, Springfield, Illinois.
- JENKINS, P. 1989. Unpublished memo written to Dr. Russell Davis, dated 15 March 1989.
- JOHNSON, A. M. 1922. An observation on the carnivorous propensities of the gray gopher [*Spermophilus franklini*]. *Journal of Mammalogy* 3: 187.
- KARASOV, W. H. 1982. Energy assimilation, nitrogen requirement, and diet in free-living antelope ground squirrels, *Ammospermophilus leucurus*. *Physiological Zoology* 55: 378-392.
- _____. 1985. Nutrient constraints in the feeding ecology of an omnivore in a seasonal environment. *Oecologia* 66: 280-290.
- KESHWI BHAT, S. 1980. Cannibalistic behaviour in captive western Ghats squirrel, *Fimambulus tristriatus* Waterhouse. *Comparative Physiology and Ecology* 5: 44-45.
- KEYMER, I. E., AND J. M. HIME. 1977. Nutritional osteodystrophy in a free-living red squirrel (*Sciurus vulgaris*). *Veterinary Record* 100(2): 31-32.
- KLUGH, A. B. 1927. Ecology of the red squirrel. *Journal of Mammalogy* 5: 1-32.
- KRULL, J. N. 1969. Observations of *Tamias striatus* feeding upon *Condylura cristata*. *Transactions of the Illinois Academy of Sciences* 62: 221.
- LANDRY, S. O., JR. 1970. The Rodentia as omnivores. *Quarterly Review of Biology* 45: 351-372.
- LARSON, E. A. 1986. Merriam's chipmunk on Palo Alto. Part II. The individual in relation to its environment. Wacoba Press, Big Pine, California.
- LEACH, D. 1977. Osteophagy in the red squirrel. *Blue Jay* 35: 102.
- LEDEBER, P. E., B. C. PIJANOWSKI AND D. L. BEAVER. 1985. Predation of tree swallows by the least chipmunk. *Jack-Pine Warbler* 63(2): 135.
- LEITNER, P. B., LEITNER AND J. HARRIS. 1991. Third year baseline report: Coso grazing enclosure monitoring study, Coso known geothermal resource area, Inyo County, California. Unpublished report dated 24 May 1991.
- MICHENER, G. R. 1982. Infanticide in ground squirrels. *Animal Behaviour* 30: 936-938.
- MOORE, J. C., AND G. H. H. TYFE. 1965. A study of the diurnal squirrels, Sciurinae, of the Indian and Indochinese subregions. *Fieldiana: Zoology*, Vol. 45. Field Museum of Natural History, Chicago, Illinois. 351 pp.
- MORGART, J. R. 1985. Carnivorous behavior by a white-tailed antelope ground squirrel, *Ammospermophilus leucurus*. *Southwestern Naturalist* 30: 304-305.
- NERO, R. W. 1987. House sparrow killed by red squirrel. *Blue Jay* 45(3): 180-181.
- NIXON, C. M., D. M. WARLEY AND M. W. McCLAIN. 1968. Food habits of squirrels in southeast Ohio. *Journal of Wildlife Management* 32: 294-305.
- O'DONOGHUE, M. 1991. Reproduction, juvenile survival and movements of snowshoe hares at a cyclic population peak. Unpublished master's thesis, University of British Columbia, Vancouver.
- OGNEV, S. I. 1966. Mammals of the USSR and adjacent countries. Vol. IV. Rodents. Israel Program for Scientific Translations, Jerusalem.
- PACKARD, R. L. 1956. The tree squirrels of Kansas: ecology and economic importance. *Miscellaneous Publications, Museum of Natural History, University of Kansas* 11: 1-67.
- _____. 1958. Carnivorous behavior in the Mexican ground squirrel. *Journal of Mammalogy* 39: 154.
- POLDER, E. 1965. Vertebrate coactions with the Franklin's ground squirrel. *Proceedings of the Iowa Academy of Sciences* 72: 202-206.
- REICHARD, T. A. 1976. Spring food habits and feeding behavior of fox squirrels and red squirrels. *American Midland Naturalist* 96: 443-450.
- ROBINSON, S. R. 1980. Antipredator behavior and predator recognition in Belding's ground squirrels (*Spermophilus beldingi*). *Animal Behaviour* 28: 540-552.
- ROEST, A. I. 1951. Mammals of the Oregon Caves area, Josephine County. *Journal of Mammalogy* 32: 345-351.
- RYAN, B. 1987. The gabar and the squirrel. *Witwatersrand Bird Club News* 136: 7.
- SANDBERG, S., AND B. H. BANTA. 1973. Instances of southern California ground squirrels (*Spermophilus beecheyi nudipes*) eating iguanid lizards. *Herpeton* 7(1): 7-8.
- SCHLOGEL, N. 1985. Eichhornchen frisst Amsel, Falke 32(9): 321.
- SETOGUCHI, M. 1990. Food habits of red-bellied tree squirrels on a small island in Japan. *Journal of Mammalogy* 71: 570-575.
- SETON, E. T. 1929. *Lives of game animals*. Doubleday, Doran and Co., Garden City, New York.
- SHACKLEFORD, N. 1966. Eastern chipmunk feeding on a starling. *Journal of Mammalogy* 47: 585.
- SHAFFER, B. S., AND B. W. BAKER. 1991. Observations of predation on a juvenile blue jay, *Cyanocitta cristata*, by a fox squirrel, *Sciurus niger*. *Texas Journal of Science* 43: 105-106.
- SHARSMITH, C. 1936. Carnivorous habits of the Belding ground squirrel. *Yosemite Nature Notes* 15: 12-14.
- SHERMAN, P. W., AND M. L. MORTON. 1979. Four months of the ground squirrel. *Natural History* 58(6): 50-57.
- SHORTBRIDGE, G. C. 1934. *The mammals of southwest Africa*. 2 volumes. William Heinemann, London.
- SMITH, C. C. 1965. The adaptive nature of social organization in the genus of tree squirrels, *Tamiasciurus*. *Ecological Monographs* 35: 31-63.
- SMITH, E. L. 1970. Cactus wrens attack ground squirrel. *Condor* 72: 363-364.
- SMITH, K. G., AND D. C. ANDERSON. 1982. Food, predation, and reproductive ecology of the dark-eyed junco in northern Utah. *Auk* 99: 650-661.
- SOWLS, L. K. 1948. The Franklin ground squirrel, *Citellus franklini* (Sabine), and its relationship to nesting ducks. *Journal of Mammalogy* 29: 113-137.

- NEDEKAR, W. AND E. M. BURTON. 1970. Food habits of the western chipmunk. California Fish and Game 76: 46-48.
- SEKI, D. 1957. On Bilibi Tik. Tattai Kora, Swara 10: 2-29.
- SORSON, L. 1953. 1953. 1953. Birds and mammals of the Sierra Nevada. University of California Press, Berkeley.
- TAYLOR, P. 1988. Population of red squirrels. Blue Jay 46: 23-97.
- TRUMBULL, JR. 1953. Stomach contents of chipmunks and mantled squirrels in northeastern California. Journal of Mammalogy 34: 316-324.
- TROTT, J. K. 1937. A chipmunk captures a mouse. Journal of Mammalogy 18: 100.
- TRUMBULL, A. W., J. LOUGHRY, D. E. HENNESSY, D. H. OWENS. 1986. Infanticide in California ground squirrels. Animal Behavior 34: 291-294.
- VILJOEN, S. 1975. Notes on the western striped squirrel *Funisciurus congicus* (Kuhl 1820). Madoqua 11(2): 119-128.
- WEEKS, H. P., AND C. M. KIRKPATRICK. 1978. Salt preferences and sodium drive phenology in fox squirrels and woodchucks. Journal of Mammalogy 59: 531-542.
- WEISSENBACHER, B. K. H. 1987. Infanticide in tree squirrels—a male reproductive strategy? South African Journal of Zoology 22(2): 115-118.
- WHITTEN, J. E. J. 1981. Ecological separation of three diurnal squirrels in tropical rainforest on Siberut Island, Indonesia. Journal of Zoology 193: 405-420.

Received 1 December 1992

Accepted 7 December 1992